Notes on echolocation calls, food and roosting behaviour of the Old World Sucker-footed bat *Myzopoda aurita* (Chiroptera, Myzopodidae)

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Abstract

In 1992 one individual of the rare species *Myzopoda aurita* was captured near Fort Dauphin in south-eastern Madagascar. Pellet analysis revealed that the animal had fed on Microlepidoptera before capture. The bat was observed in a flight cage. It clinged head upright to the lower leaf surface of a traveller's palm *Ravenala madagascariensis*, using its stiff tail as a prop. While readily flying in the cage, the specimen emitted FM echolocation calls which were recorded and analysed for the first time in this species: They are characterized by two to four distinct pulse elements of increased amplitude. The second of maximal four harmonics was always the strongest component. During the remarkably long call of up to 23 ms, the frequency of the second harmonic decreased from 42 to 24 kHz with a shallow sweep at the beginning and a steep sweep at its end. Most calls were emitted in pairs. Possible functions of this call structure are discussed.

Introduction

The "old world sucker-footed bat" *Myzopoda aurita* (Milne-Edward and Grandidier, 1878) is the only representative of the monotypic family Myzopodidae, endemic to Madagascar. This species shows remarkable morphological specializations like sucking disks on thumbs and feet, long ears with unique mushroom-shaped processes, elongated palate and projecting tail, all indicating a long isolated evolution (reviewed by Schliemann and Maas 1978). *M. aurita* seems to be very rare: Schliemann and Maas (1978) estimated less than 15 records of its existence, most dating before 1900. Since then, a few specimens have been recorded during expeditions by Cambridge and Aberdeen Universities and the Smithsonian Institute (Safford and Duckworth 1990 and unpublished data). Due its rarity, there is still no information about the biology of this bat. Only the use of the sucking disks in *M. aurita* is indicated by one specimen collected by Hoogstral in 1947 (unpublished data) from smooth leaves of the traveller's palm *Ravenala madagascariensis* (Musaceae), which served as a roost (Schliemann and Maas 1978). However, no further details concerning roosting behaviour have been reported.

Although echolocation calls of representatives of nearly all bat families have already been recorded (Sales and Pye 1974; Novick 1977), calls of *M. aurita* are still unknown. The same applies to nutrition. Because the dentition is of the normal insectivorous type (Thomas 1904), *M. aurita* has been assumed to feed on insects, but this has not yet been confirmed.

During an expedition in 1992, we captured one individual and collected some data about echolocation calls, food, and roosting behaviour.

Material and methods

On August 13, 1992 a female *M. aurita* was captured with mist nets at Antanifotsy, 8 km north of Fort Dauphin in southeastern Madagascar. The nets were installed at the border of a rice field near the village at the base of the coastal mountains. In the surroundings, remains of primary forest were limited to inaccessible ravines and the upper regions of mountain slopes, while the lower areas were cleared. Wide marshlands extended between the village and the coast. Traveller's palms were common in primary and secondary forests. In the following weeks no other specimen was found, although up to 6 mist nets have been set up almost every night in the surroundings and several palms have been checked for roosting *M. aurita*.

The bat was trapped at a height of 1.5 meters above ground at 18.55 h local time about one hour after sunset. The following measurements were taken: forearm length 48 mm, head-body length 62 mm, tail 48 mm, ear 33 mm. The nipples of the female were well developed. After capture it was kept in a bag for a few hours to collect fecal pellets and then in a cage of two meters side length for two nights. For roosting, *Ravenala* leaves were installed in the cage and the bat had the opportunity to feed on free-flying and hand-held mosquitoes, Microlepidoptera, and larger moths.

Echolocation calls of the flying bat were recorded in the cage with a QMC PSM3 microphone on a modified Panasonic video recorder. For evaluation, calls were recorded with a RACAL store DS tape recorder and after appropriate slow down (mostly 16×) analysed with a MOSIP-FFT-processor (Fa. MEDAV, Erlangen, Germany). Spectrograms presented in the present study are copies of the originals in which echos have been removed.

40 fecal pellets were collected after capture. They were stored dry and later analysed in ethanol (70%).

Results

Behaviour and food

Caged, the bat spontaneously used leaves of the traveller's palm *Ravenala madagascarien-sis* for roosting. The bat preferred to cling head upright to the surface of the leaves with help of all four sucking disks, using the stiff, projecting tail as a prop (Fig. 1). It even climbed on the lower surface with its dorsum downwards, if the leaf was bended horizontally by the bat's weight. After sunset, it performed a highly manoeverable flight but was never observed to pursue free-flying insects, nor did we succeed to feed it.

The 40 analysed fecal pellets contained only remnants of Microlepidoptera, identified by the dimensions and structure, especially of head, leg and wing fragments, with scale insertions and great quantity of scales. A more specific determination was not possible.

Echolocation calls

While flying in the cage, the bat emitted complex frequency modulated (FM) echolocation calls remarkable for each being composed of two to four distinct elements of increased amplitude and long call durations. Due to different numbers of elements and the presence of up to four harmonics, the call structure was highly variable.

Most calls (65%, n = 85) were composed of four elements (Fig. 2 a, b): The amplitudes of the four elements varied: The fourth element showed the highest amplitude in 81% and the fourth and second at nearly same levels in 13% of the calls. While the fourth element was always loud, high amplitude levels of the other elements were observed more rarely.

Frequencies decreased from the first to fourth element. Thus, the elements are characterized by different frequency ranges and maximum amplitudes at specific frequencies

Fig. 1. *Myzopoda aurita* resting on the lower surface of the leaf of a traveller's palm *Ravenala madagascariensis* in captivity.

(Tab. 1). In each element serveral harmonics could be present and the second harmonic was always the strongest component. Considering all elements, the second harmonic decreased from 42 to 24 kHz with a shallow FM sweep (about 0.6–0.9 kHz/ms) during the first three elements and a steep FM sweep (about 2 kHz/ms) during the fourth element. Due to low amplitude components between the peaks, a pulsed sweep resulted with four amplitude peaks in the second harmonic (Fig. 2 a, b). The first harmonic was much weaker and was only observed in some elements of about half of the calls (Fig. 2 a, c, Fig. 3). According to its low amplitude, it was often limited to amplitude peaks of elements. A third harmonic was found in the last element of only seven calls (Fig. 2 b) and two times in the second, while a fourth harmonic was present in nearly half of the calls in the last and more rarely in the second and third elements (Fig. 2 b). Although the frequency range above 80 kHz has been examined, a fourth harmonic was never observed in the first element.

The remainder of the analysed calls was composed of only two (9%) or three (26%) elements. In comparison to calls with four elements, in these calls the first and third elements could be absent (e. g. in the second and fourth call in Fig. 3) or elements were fused as indicated by frequency spectra. The call presented in figure 2 c, for example, shows fused second and third and barely separated first and fourth elements resulting in continuous sweeps from 20 to 18 kHz in the first harmonic and from 38 to 24 kHz in the second one. In addition, a fourth harmonic is visible in the last element.
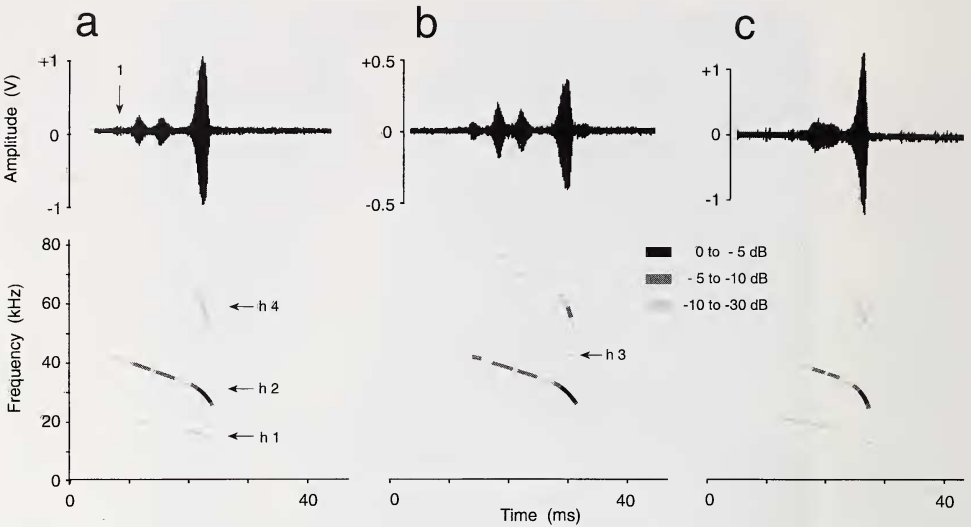
Fig. 2. Single echolocation calls of *Myzopoda aurita*. Relative sound pressure levels from 0 (= loudest) to −30 dB below maximum are shown. h1–h4: first to fourth harmonic. a: Call composed of four elements (arrow 1: hardly visible first element), with pronounced second harmonic. In the fourth element the first and fourth harmonics are visible; b: Call composed of four elements. In addition to a pronounced second harmonic third and fourth harmonics are visible. A first harmonic is not detectable; c: Call composed of three elements resulting from a call with four elements by fusion of second and third elements.

An impression of the high variability resulting from emission of different numbers of elements and different amplitudes of harmonics is given in figure 3, showing a call sequence of four calls presented in two pairs. Four elements are present in the first and third, three in the fourth and two in the second call. There are also differences concerning the presence of the first and fourth harmonics.

Durations of 85 analysed calls varied between 12 and 23 ms (Fig. 4). While durations of calls composed of two or three elements did not differ significantly ($p > 0.05$; median-test), durations of calls with four elements were shifted to longer times ($p < 0.01$; median-test). Call intervals lasted between 11 and 108 ms and showed a bimodal distribution (Fig. 5): during most of the recording time calls were emitted in pairs with only short intervals between the two calls of one pair (25 ± 5 ms, n = 32) and longer intervals between different pairs (69 ± 10 ms, n = 28).

Table 1. Peak frequencies and frequency ranges of the four elements and four harmonics in 85 analysed calls of *Myzopoda aurita*. In some elements the third and fourth harmonics were visible as amplitude peaks. Therefore, only peak frequencies are presented. *: not visible in spectrograms of analysed calls.

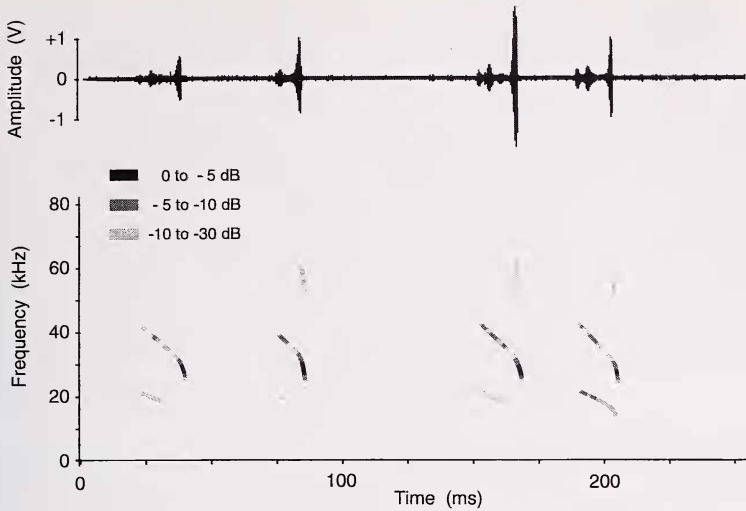| harmonics	elements				frequency range (kHz)
	1	2	3	4	
	peak frequencies (kHz)				
1	20	19	18	14	14-21
2	41	38	35	29	24-42
3	*	57	*	43	(43/57)
4	*	76	70	58	50-64 (70/76)

Fig. 3. Continuous call sequence consisting of four calls emitted in two pairs. Note the high variability concerning numbers of elements in calls and presence of first and fourth harmonics.
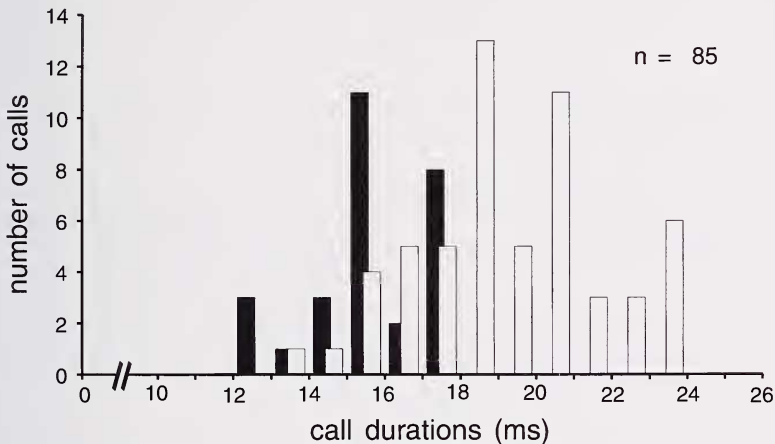

Fig. 4. Distribution of call durations in *Myzopoda aurita*. Calls composed of four elements (white) show longer durations than calls composed of two or three elements (black).

Discussion

Distribution, behaviour and food

Previous records of *Myzopoda aurita* indicate that the species is distributed mainly along the east coast of Madagascar. The locality of our record fits with this distributional pattern, for several specimens have already been captured in the northern vicinity of Fort Dauphin (SCHLIEMANN and MAAS 1978 and unpublished records of Smithsonian Institute in 1989).

Roosting behaviour of *M. aurita* is indicated by one specimen collected from leaves of the traveller's palm *Ravenala madagascariensis*, but no further details have been reported
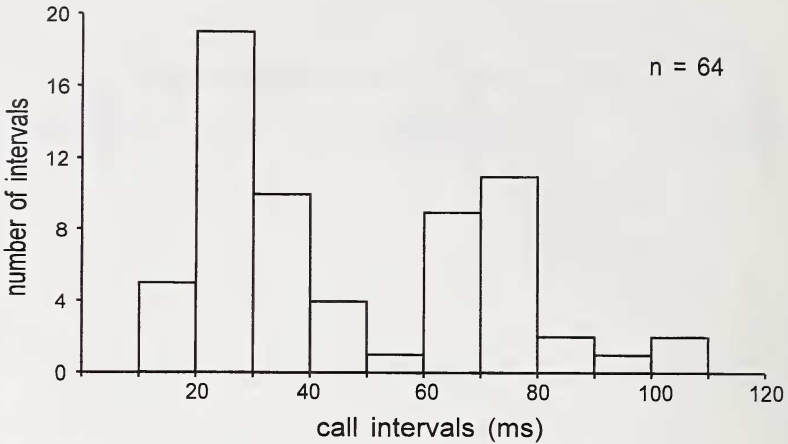
Fig. 5. Distribution of call intervals in *Myzopoda aurita*. Calls were mostly emitted in pairs causing a bimodal distribution.

(Schliemann and Maas 1978). *Ravenala* is abundant and is possibly used as a roost in the surroundings of the capture site, but other plants providing large smooth leaves such as Araceae are also common. We observed that caged *M. aurita* uses its adhesive disks to cling to leaves of *Ravenala* and that adhesion is sufficient to carry the entire weight of the bat. A head upright roosting position as shown by the presently described individual has also been reported for the New World sucker-footed bats (Thyropteridae, Nowak 1991). The stiff, projecting tail of *M. aurita* is used as a prop comparable to the use of the tail in woodpeckers.

The examined pellets of the captured bat contained fragments of Microlepidoptera. This confirms earlier assumptions that this species feeds on insects deduced from dental characters (Thomas 1904). The occurrence of Microlepidoptera in the diet may be an indication of specialization or a mere result of accidental abundancy of this type of prey at that time. As most sound energy of the calls of *M. aurita* lies within the frequency range known to be conspicuous to many tympanate moths (Fenton and Fullard 1979), the feeding on Microlepidoptera may also be explainable with the absence of tympana in most microlepidopteran families (exept e. g. Pyralidae).

Echolocation calls

The echolocation calls recorded of *M. aurita* flying in a cage show some pecularities: They are complex FM echolocation calls remarkable for long durations and for composition of two to four elements. Each element contains several harmonics and the second harmonic is always the strongest component. Frequencies decrease in the course of the call resulting in an pulsed sweep, which is shallow during the first three elements and steep during the last, mostly loudest element.

Call durations can be influenced by recording conditions: In the field, even longer durations can possibly be expected considering that in captivity a reduction of call durations has been reported for several species, probably as an adaptation to short distances (e. g. Griffin 1958; Novick 1977; Kalko and Schnitzler 1989). The pulsed pattern of the calls cannot be attributed to frequency characteristics of the recording equipment: In calls of other bat species with similar frequency spectra that have been recorded with the same equipment under the same circumstances, no such effect is visible.

The long, shallow sweep and the short, steep sweep at the end of the call are appropriate for the detection of different characteristics of the target according to the optimal filter theory (GLASER 1974):

Long, shallow sweeps are interpreted to function as long-distance probes (NEUWEILER 1983) and to be utilized for recognition of fluttering targets (SCHNITZLER 1987). A long-distance probe can be achieved by packing sound energy in a shallow sweep, if it lies within the critical band (NEUWEILER 1983). Considering call durations and average frequency decrease, the calls of *M. aurita* are comparable to those of Molossidae (estimated from data presented by FENTON and BELL 1981). Molossids are assumed candidates for detection of fluttering targets. In this family an increased probability of target detection has been demonstrated, when amplitude glints originating from the moving insect are present in the echos (SCHNITZLER 1987). While the shallow sweep in calls of *M. aurita* can possibly be used for detection of insect wing beats, their high-amplitude modulated calls seem to be rather disadvantageous for the detection of amplitude glints.

Short, steep sweeps as emitted at the end of the call show a broader bandwidth and are therefore favourable for measuring the distance to discrete targets (GLASER 1974). The last element may also be used for target detection, because it always combines high amplitudes with low frequencies, which are less affected by atmospheric attenuation than the higher frequencies at the beginning of the call.

Complex calls composed of two elements have already been reported from other bat species. In contrast to *M. aurita*, these calls often show two amplitude maxima at the same frequency, and pulsation is caused by changes in energy distribution between different harmonics (SALES and PYE 1974). A pulsed structure as emitted by *M. aurita* has hitherto not been described. Therefore, only some hypotheses about possible functions can be presented:

The pulsations could offer time markers to measure the distances to targets, a function that is considered for the slopes of intensity envelopes (NEUWEILER 1983).

Assuming a limitation of total energy disposable for one call, pulsed calls might be emitted to increase the amplitudes of specific frequencies by temporal concentration of sound energy. Thus, the distances from which echos can be recognized are increased for specific frequencies. In addition, the entire echo might be more conspicuous due to the characteristic temporal pattern of a pulsed call.

The use of pulsed calls to measure flight speeds of insects by comparing the echo delays at the distinct amplitude peaks of one call is rather improbable: During one call, movements of flying insects are short and the resulting echo delays are often shorter than minimal time differences detected by other bat species (SIMMONS 1973).

The pulsation of calls could also enable the bat to adapt its calls to different conditions by pronouncing different elements and therefore portions of different sweep ratios and different frequencies, as indicated by the variability of the relative amplitudes of the distinct elements. For a detailed interpretation of the function of this pulsed call structure and the echolocation abilities of *M. aurita* echolocation calls have to be recorded in the field and details about foraging behaviour should be observed.

Acknowledgements

Zusammenfassung

Echoortungssignale, Nahrung und Gebrauch der Haftorgane von Myzopoda aurita (Chiroptera, Myzo-
podidae)

Ein Exemplar der seltenen Art *Myzopoda aurita* wurde 1992 bei Fort Dauphin im Südosten Madagas-
kars gefangen. Kotprobenanalysen ergaben, daß das Tier vor dem Fang Microlepidopteren gefressen
hatte, und belegen damit erstmals die Insektivorie der Art. In einem Flugkäfig wurde beobachtet, daß
sich *M. aurita* zum Schlafen mit nach oben gerichtetem Kopf an Blattunterseiten von *Ravenala mada-*
gascariensis mit den Haftscheiben festsaugt, wobei der Schwanz als Stütze dient. Während das Tier wen-
dig im Käfig flog, wurden erstmals Echoortungssignale der Art aufgezeichnet: Die Rufe weisen
auffällige, regelmäßige Amplitudenmodulationen auf, die die Rufe in zwei bis vier Elemente gliedern.
Von maximal vier sichtbaren Harmonischen ist die zweite am deutlichsten: Während der maximal 23 ms
langen Rufe sinken die Frequenzen der zweiten Harmonischen von 42 bis 24 kHz. Die Rate der Fre-
quenzmodulation ist gering, nur am Rufende tritt ein breitbandiger FM-Teil auf. Die Rufe wurden
meist paarweise abgegeben. Die Signalstruktur wird im Hinblick auf mögliche Ortungsleistungen disku-
tiert.

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